

Population Structure, Life Cycle and Habitat of the Pondweed Bug *Mesovelvia furcata* (Hemiptera, Mesoveliidae) * ¹

by

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With 4 Figures and 8 Tables

ABSTRACT

Population structure and life cycle of the pondweed bug *Mesovelvia furcata* (Hemiptera, Mesoveliidae) were investigated on three ponds in the region of Berne (Switzerland). Laboratory reared specimens supported the observations made in the field.

Field samples (about 3000 nymphs), mass cultures of the different instars and, above all, individual rearings from hatching, revealed that *M. furcata* (both wingless and winged specimens) has but four nymphal stages, a number unusual for semiaquatic Hemiptera (Gerromorpha).

M. furcata was clearly trivoltine. Total population density increased from first to third generation and by mid-August amounted to some 600 bugs per sqm on one of the study ponds.

M. furcata hibernate as eggs in embryonic diapause, the germ band, immersed in the yolk, having assumed an elongated S-shape. Females of the first generation taken to the laboratory (24° C, 18L:6D) laid, without exception, nondiapause eggs. Those of the second generation already laid diapause eggs (about 50%), but the proportion of nondiapause eggs was much higher than in females of the third generation, which laid mainly diapausing eggs. Eggs hibernate in stems of rooted plants of the emergent zone, both above and below the water surface, and also, but less frequently, in rotting plants at the bottom of ponds. A first account of an hymenopteran egg parasitoid (*Anagrus incarnatus subfuscus* Hal., Mymaridae) of *M. furcata* is given.

* Part of the author's thesis.

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M. furcata is strongly associated with plants of the water lily communities (Nymphaeion). In most habitats *Nymphaea alba*, *Nuphar lutea*, or *Potamogeton natans* were present.

INTRODUCTION

The small family Mesoveliidae (water treaders), with about 35 known species in 10 genera, has a world-wide distribution (ANDERSEN & POLHEMUS 1980, MALIPATIL & MONTEITH 1983). Virtually all of the palaeartic species belong to the cosmopolitan genus *Mesovelia*, the only exception being *Speovelia maritima*, an endemic on Japan and Ryukyu Islands. Typical habitats of most species are still waters with abundant swimming vegetation. A few species, however, prefer more hidden habitats e.g. moss covered rocks, gravel and stones along river-banks, and *M. amoena* (= *M. douglasensis*) on Hawaii is even known to be cavernicolous (HUNGERFORD 1917, SCHUMACHER 1919, POISSON 1933, 1957, GAGNE & HOWARTH 1975, POLHEMUS & CHAPMAN 1979, ANDERSEN & POLHEMUS 1980, ANDERSEN 1982, a.o.).

Three European species are known: *M. furcata*, *M. thermalis* and *M. vittigera*. Adults of these three species are morphologically easily discernible (HORVATH 1915, STICHEL 1955, POISSON 1957, NIESER 1982). The only place where *M. thermalis* has been found so far, is the thermal lake of Püspökfürdő near Oradea in Rumania (HORVATH 1915, 1929, ANDERSEN & POLHEMUS 1980). Within Europe *M. vittigera* (= *M. orientalis*) is confined to the Mediterranean countries (HORVATH 1929, POISSON 1933, STICHEL 1955, BAENA RUIZ 1982, NIESER 1982). Its whole distribution however extends from Africa to the Samoa Islands (ANDERSEN & POLHEMUS 1980). In Central Europe only *M. furcata* is found. Records from most European countries exist and the range of distribution covers the greater part of the Palaeartic (HORVATH 1929, STICHEL 1955, ANDERSEN & POLHEMUS 1980). The presence of *M. furcata* in our country, oddly enough, was discovered only quite recently by DETHIER & MATTHEY (1977). They mention four localities in the region of Lausanne and lake Neuchâtel, and a further population was found in the Canton of Fribourg by ZURWERRA (1978). Despite of its wide occurrence, the local distribution of *M. furcata* is not much known, probably because of its small size, cryptic colour and inconspicuous behaviour (SCHUMACHER 1919, JORDAN 1931, 1952, POISSON 1933, WESENBERG-LUND 1943).

Starting with BUTLER (1893), quite a few papers on the biology of *M. furcata* were published (LUNDBLAD 1915, 1916, 1916a, JANSSON 1916, MUELLER 1919, SCHUMACHER 1919, TEYROVSKY 1920, BUTLER 1923, EKBLUM 1930, JORDAN 1931, 1952, SOUTHWOOD & LESTON 1959, COBBEN 1965, 1968, DETHIER & MATTHEY 1977, ANDERSEN 1982, NIESER 1982). This led POISSON, already in 1933, to the conclusion that the biology of *M. furcata* was well known. This statement must, however, be denounced as an exaggeration. There is still no general agreement about voltinism, phenology and hibernating stage of *M. furcata* (NIESER 1982). The pondweed bug is described to be either, univoltine (EKBLUM 1930, JORDAN 1931, 1952, DETHIER & MATTHEY 1977, TAMANINI 1979, a.o.) or at most bivoltine (TEYROVSKY 1920, SOUTHWOOD & LESTON 1959, GALBREATH 1975). It is assumed that overwintering takes place within the egg in an embryonic diapause (EKBLUM 1930, SOUTHWOOD & LESTON 1959, ANDERSEN 1982) or else in quiescence (COBBEN 1968). Other authors state that adults (JORDAN 1931, 1952, TAMANINI 1979) or only mated females hibernate (TEYROVSKY 1920).

The aim of the present study is to answer the following questions:

- How many generations are produced per year by *M. furcata*?
- Which is the hibernating stage of the pondweed bug?
- Is the overwintering stage in diapause or only quiescent?
- What about the regional distribution of this water surface dweller?

MATERIALS AND METHODS

All data presented in this preliminary study of the biology of *M. furcata* were collected from March 1983 to April 1984. They comprise field observations as well as results of laboratory rearings.

STUDY SITES: Population structure and life cycle of *M. furcata* were studied on three different ponds. Two of them (A and B of this paper) are situated within the nature reserve Auriéd (FR) near Laupen (BE), the third (C) is a newly dug ornamental pond in front of our Zoological Institute in Berne. In 1978 ZURWERRA discovered *M. furcata* in the Auriéd and subsequently we found the populations on several ponds to be quite dense at times. A description and notes on the development of the nature reserve are given by ZURWERRA (1978). Our samples from pond A (pond 4 of ZURWERRA) were taken from the southern shore, where the vegetation consisted of a rich growth of emergent plants, such as *Typha sp.*, *Sparganium sp.*, *Alisma plantago-aquatica*, *Carex sp.*, *Mentha aquatica* etc., and a three to five meters wide belt of floating broad leaved pondweed (*Potamogeton natans*). On pond B (6 of ZURWERRA) no such floating zone existed. There were only small mats of swimming algae. This pond was open to the sun, whereas pond A was quite shady due to surrounding bushes. Pond C (in front of our Institute) was constructed in 1982, and, among others, the following plants were introduced in the autumn of the same year: water liliés (*Nymphaea sp.*, *Nuphar lutea*), *P. natans*, bur-reed (*Sparganium sp.*), reedmace (*Typha sp.*), water plantain (*A. plantago-aquatica*), sedges (*Carex sp.*), true bulrush (*Scirpus lacustris*), *Hippuris vulgaris*, rushes (*Juncus sp.*), and yellow iris (*Iris pseudacorus*).

In order to get a picture of the frequency of occurrence and the pattern of distribution of *M. furcata* in our region, many ponds between Solothurn and Fribourg were screened mainly in August and September 1983. On these ponds other surface dwellers, as well as the principal, submerged and swimming plants were recorded.

SAMPLING AND STATISTICS: Samples were taken within reach from the shore by placing a wooden frame (50×50 cm) on the water, and collecting all the enclosed specimens. The insects were brought to the laboratory in a cooling box. For inspection, and prior to preservation in 70% ethanol, they were anaesthetized with CO₂.

To determine the stages and for biometrical recordings, a dissecting microscope, fitted out with an eye piece micrometer, was used. In March and April pond A was inspected every fortnight, and from May to October weekly (the two other populations were monitored less periodically). The following relates to pond A only. In July and August 4 frames (1 m²) were sampled each time. The frame was deposited as follows: 1) next to the shore; 2) in the zone of emergent vegetation; 3) in the centre of the floating zone and 4) at the outer edge of this zone. Before July and after the end of August sampling effort was not standardized in the above mentioned way. An attempt was made to catch about forty individuals each time. That sample size was big enough to be representative. Stage-specific survival rates, stage durations and numbers entering the different stages were computed according to the method of KIRITANI & NAKASUJI extended by MANLY (1976). We already

used this method successfully in our population study of *Gerris lacustris* (ZIMMERMANN *et al.* 1982).

From December to April several samples of emergent and submerged parts of rooted plants, as well as of plants rotting at the bottom of the ponds, were brought to the laboratory, and inspected for hibernating eggs of *M. furcata*.

LABORATORY REARINGS: Mass cultures and individual rearings were performed under an artificial photoperiod (18L:6D) and a temperature of about 24° C (range: 22,5—25° C). Field sampled adults were bred in polyethylene tanks (20×25×15 cm). Small pieces of styrofoam were put on the water as oviposition sites. Both adults and nymphs were fed in abundance with frozen *Drosophilae* and occasionally with some Calliphoridae. Newly moulted individuals and exuviae were counted daily; exuviae were put into 70% ethanol, and the newly moulted specimens were transferred, using a small sieve, into another box in order to keep the different stages separated. Individuals could be reared singly, from hatching to adulthood, on distilled water in small circular plastic boxes (∅ 6 cm, h 3 cm), placed on an earthed metal plate to prevent electrostatic charging. Diapausing eggs were kept for variable time periods in a fridge (T=4° C).

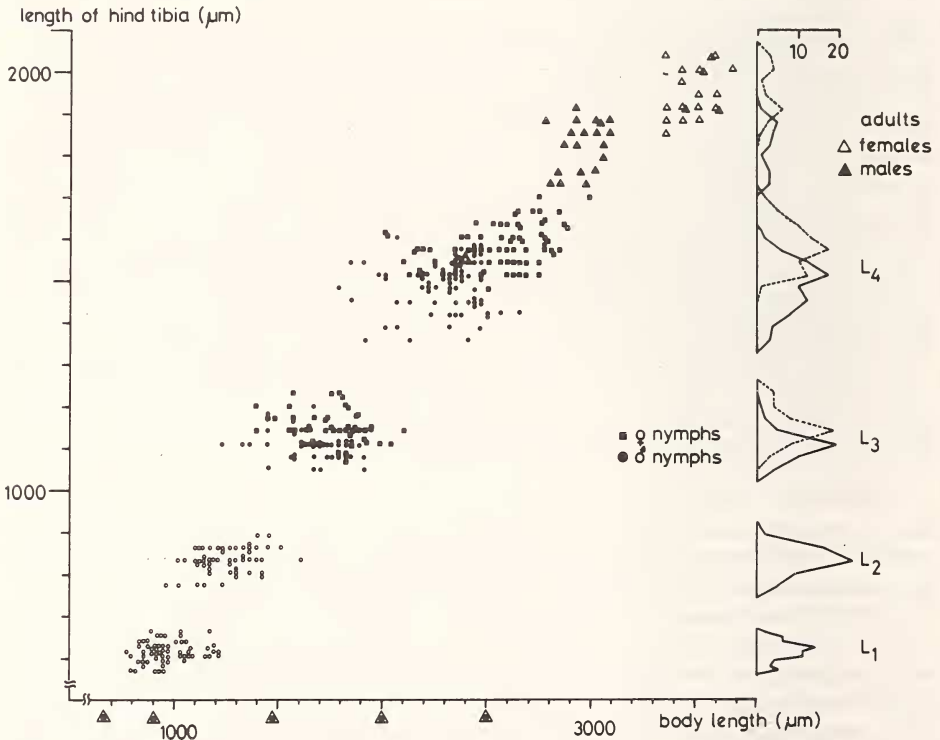


FIG. 1.

Length of hind tibia in relation to body length from first instar nymphs (L1) to adults.

The sexes are discernible from the third instar on the morphology of the 8th and 9th abdominal sternite.

\triangle body length as given by JORDAN (1931)

\blacktriangle our measurements taken from a male last instar nymph depicted by ANDERSEN (1982).

RESULTS

NUMBER OF NYMPHAL INSTARS

The usual number of nymphal instars in semiaquatic bugs (Gerromorpha) is five (SCHOUTEDEN 1921, BERTRAND 1954, POISSON 1957, TAMANINI 1979, ANDERSEN 1982 a.o.). A few species have reduced this number to four, e.g. *Mesovelia cryptophila* (HOFFMANN 1932), *Rhagovelia obesa* (CHENG & FERNANDO 1970) and several members of the genus *Microvelia* (FRICK 1949, DON 1967, ANDERSEN 1982).

M. furcata has been considered to belong to the great majority with five preimaginal instars (TEYROVSKY 1920, SCHOUTEDEN 1921, EKBLUM 1930, JORDAN 1931, 1936, ANDERSEN 1982 a.o.). JORDAN (1931) gives a description of the five stages, which, according to him, differ in body length. Our biometrical analysis of field samples (more than 300 instars measured out of 3000 nymphs sampled), mass laboratory cultures (more than 150 adults obtained), and above all direct counting of moults in individual rearings from hatching to adulthood (20 successful cases out of 221 attempts), conclusively demonstrate the existence of only four preimaginal instars in *M. furcata*. This holds both for wingless and winged specimens. Fig. 1 shows a clear difference with no overlap between the length of hind tibiae of the nymphal stages, but at the same time the non-suitability of body length as a criterion for separating the stages. Other measures too, e.g. the head width, and morphological features, such as chaetotaxy and other structures of the body segments, characterize the four instars. A detailed description of the nymphs will be published elsewhere (ZIMMERMANN in prep.).

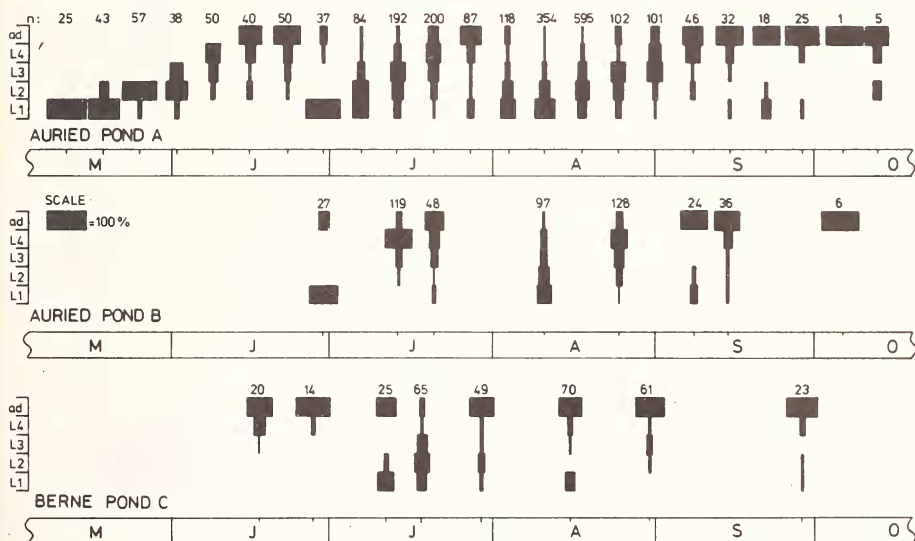


FIG. 2.

Population structure of *M. furcata* on the three ponds under study.
 n: sample size; L1-L4: the four nymphal stages; ad.: adults.
 The exact numbers, of the different instars sampled, are given in Table 1.

POPULATION STRUCTURE AND LIFE CYCLE

Results of our observations are summarized in Table 1 and Fig. 2. Specimens of *M. furcata* were found on pond A from the beginning of May to mid-October. In March and April, when adults of *Microvelia reticulata* and *Gerris argentatus* were already abundant on the water, not a single nymph or adult of *M. furcata* was seen. The first individuals belonging to this species caught in May were, without exception, first instar nymphs. At the same time, the first nymphs of *G. argentatus* made their appearance. During May, the number of first instar nymphs of *M. furcata* quickly diminished and gradually the higher instars appeared. Adults of this first generation were first observed by mid-June and proved to be abundant for only about a fortnight. They readily reproduced by implanting their eggs into stems and leaves of floating and of emergent water plants. Specimens of *P. natans*

TABLE 1.

Population structure on pond A. n: number of individuals of the respective instars.

The horizontal lines separate the three generations. Test on even sex ratio:

no sign: not significant; *1% < P < 5%; ** P < 1%.

| Date | L1 | | L2 | | | L3 | | | L4 | | | Adults | | | Sample size |
|--------|-----|-----|-----|----|-----|----|----|-----|----|----|------|--------|----|---|-------------|
| | n | n | ♂♂ | ♀♀ | n | ♂♂ | ♀♀ | n | ♂♂ | ♀♀ | n | ♂♂ | ♀♀ | n | |
| 11.5. | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 |
| 18.5. | 34 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 43 |
| 25.5. | 7 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 57 |
| 1.6. | 1 | 23 | 5 | 9 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38 |
| 8.6. | 0 | 4 | 3 | 7 | 10 | 21 | 15 | 36 | 0 | 0 | 0 | 0 | 0 | 0 | 50 |
| 15.6. | 0 | 4 | 1 | 1 | 2 | 7 | 3 | 10 | 11 | 13 | 24 | 0 | 0 | 0 | 40 |
| 22.6. | 0 | 3 | 0 | 4 | 4 | 4 | 4 | 8 | 18 | 17 | 35 | 0 | 0 | 0 | 50 |
| 29.6. | 32 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 4 | 4 | 0 | 0 | 0 | 37 |
| 6.7. | 35 | 35 | 4 | 8 | 12 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 84 |
| 13.7. | 30 | 57 | 28 | 34 | 62 | 18 | 12 | 30 | 10 | 3 | 13 | 0 | 0 | 0 | 192 |
| 20.7. | 3 | 25 | 21 | 26 | 47 | 45 | 28 | 73* | 35 | 17 | 52* | 0 | 0 | 0 | 200 |
| 27.7. | 13 | 5 | 4 | 2 | 6 | 9 | 6 | 15 | 32 | 16 | 48* | 0 | 0 | 0 | 87 |
| 3.8. | 45 | 37 | 6 | 8 | 14 | 4 | 5 | 9 | 7 | 6 | 13 | 0 | 0 | 0 | 118 |
| 10.8. | 195 | 115 | 20 | 12 | 32 | 4 | 2 | 6 | 5 | 1 | 6 | 0 | 0 | 0 | 354 |
| 17.8. | 138 | 197 | 100 | 81 | 181 | 29 | 32 | 61 | 12 | 6 | 18 | 0 | 0 | 0 | 595 |
| 24.8. | 15 | 28 | 16 | 16 | 32 | 9 | 3 | 12 | 11 | 4 | 15 | 0 | 0 | 0 | 102 |
| 31.8. | 3 | 12 | 17 | 14 | 31 | 15 | 12 | 27 | 21 | 7 | 28** | 0 | 0 | 0 | 101 |
| 7.9. | 0 | 2 | 1 | 0 | 1 | 8 | 10 | 18 | 12 | 13 | 25 | 0 | 0 | 0 | 46 |
| 14.9. | 2 | 0 | 1 | 1 | 2 | 2 | 1 | 3 | 20 | 5 | 25** | 0 | 0 | 0 | 32 |
| 21.9. | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 1 | 13** | 0 | 0 | 0 | 18 |
| 28.9. | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 12 | 10 | 22 | 0 | 0 | 0 | 25 |
| 5.10. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| 12.10. | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 3 | 0 | 0 | 0 | 5 |

TABLE 2.

Estimates of survival rates, stage durations and numbers entering the different instars of the second generation.

| | survival rate \pm s.e. | stage duration (in days) | number entering stages (per sqm) |
|-------|-----------------------------|-----------------------------|-------------------------------------|
| L1 | 0,84 \pm 0,03 | 1,6 | 472 |
| L2 | 0,76 \pm 0,05 | 2,5 | 395 |
| L3 | 0,68 \pm 0,08 | 3,6 | 301 |
| L4 | 0,50 \pm 0,10 | 6,4 | 204 |
| adult | - | - | 102 |

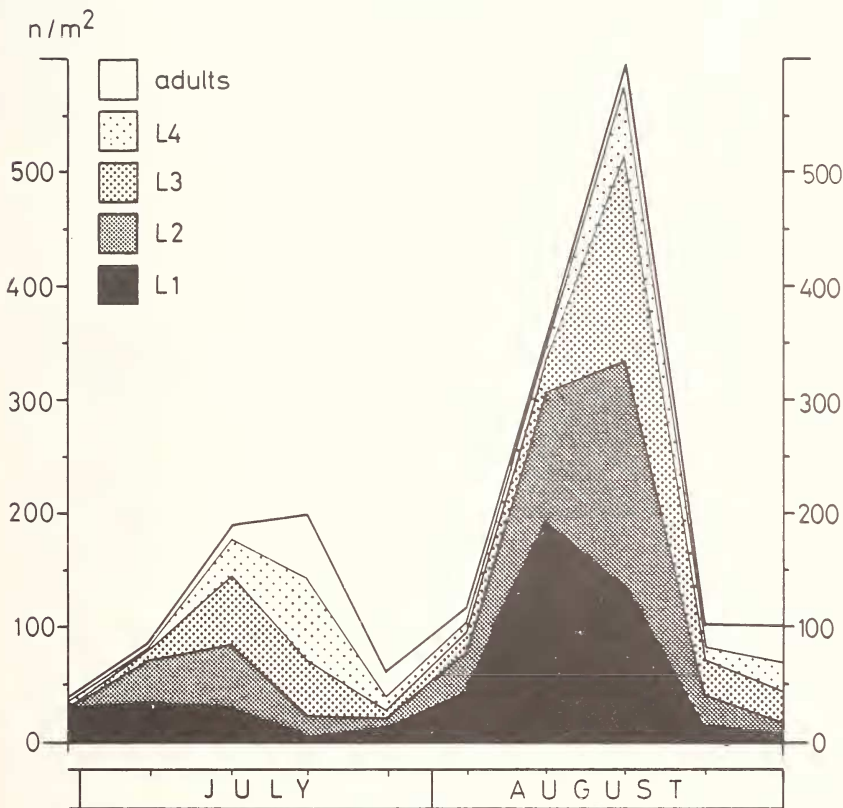


FIG. 3.

Density of the different instars and total population density as estimated from quadrat sampling ($1 m^2$).

and *M. aquatica*, brought to the laboratory on the 22nd June, contained eggs which hatched within a week. On pond A, second generation nymphs appeared from the end of June and developed into adults within two to three weeks. By the end of July a further increase in first instar nymphs indicated the onset of a third generation, whose first adults emerged by mid-August. From September onwards adults of this third generation clearly outnumbered the nymphs. A small number of young nymphs (L1, L2), probably representing a potential partial fourth generation, observed in the second half of September, obviously did not succeed in completing development before winter set in. The findings on the ponds B and C coincide with those made on pond A.

Total population density markedly increased from the second to the third generation (Fig. 3). By mid-August, it amounted to some 600 individuals per sqm, and the population consisted mainly of L1, L2 and L3. From June to October, density of adults was always much lower than 100 individuals per sqm. Several samples showed a great excess of male adults although among nymphs sex ratio was generally well-balanced (Table 1).

The estimates of stage specific survival rates, stage durations and numbers of individuals entering the different stages are summarized in Table 2. Overall survival (L1 to adult) of 2nd generation nymphs was about 20%.

Three samples of adults from June 15th, July 20th and August 30th were used for mass culture. Females of *M. furcata* lay their eggs, with the aid of a well developed serrate ovipositor, into plant tissue (TEYROVSKY 1920, EKBLUM 1930, JORDAN 1931, 1952 a.o.). In the laboratory, they quite willingly insert their eggs into styrofoam (COBBEN 1968) where they can be inspected easily. Eggs differ in their capacity for immediate development (Table 3).

TABLE 3.

Direct or postponed development of eggs laid by females of the three successive generations. Nondiapause eggs hatch within two to three weeks, whereas diapause eggs suspend development at a distinct stage even under favourable conditions.

| | nondiapause eggs | diapause eggs | total |
|--|------------------|---------------|-------|
| 1st generation (24°C; 18L:6D) | 121 | 0 | 121 |
| 2nd generation (24°C; 18L:6D) | 288 | 318 | 606 |
| 3d generation (24°C; 18L:6D) | 78 | 486 | 564 |
| 3d generation (outdoors from 31.8. to 12.10) | 0 | 383 | 383 |

Those of the females of the first generation all developed into first instar nymphs within two to three weeks. Only about half of the eggs laid by 2nd generation females developed in this way, the rest suspended development at a distinct stage and only resumed it after a period of diapause. Diapause begins when the germ band, being immersed in the yolk, has assumed an elongated S-shape. The protocormic appendages are not yet formed and red symbionts (COBBEN 1965, 1968) form a light reddish circle beneath the pseudopericulum. Females of the third generation kept outdoors laid only diapause eggs. Diapause could be terminated by a chilling period of six weeks ($T=4^{\circ}\text{C}$). Transferred to a temperature of 24°C these eggs hatched synchronously within 16 to 19 days. Photoperiod obviously does not affect diapause termination, since two samples of diapause eggs, transferred from 4°C to 20°C , and kept under two photoperiods of 18L:6D and 10L:14D respectively, hatched within the same time interval.

In nature diapause eggs were found from the beginning of September (Table 4). They were inserted into both emergent and submerged parts of several species of water plants, such as *Typha sp.*, *Sparganium sp.*, *Scirpus lacustris*, *Iris sp.*, *Carex sp.* and *Mentha aquatica*. Eggs found below, as well as above the water surface, could be kept alive under our standard laboratory conditions (24°C) and hatched quite readily, but far less synchronously than laboratory-laid eggs.

TABLE 4.

Hibernating eggs found in field samples. In brackets: number of plants inspected; —: no plants sampled.

| Date, Locality | rotting, submerged plants | rooted, erect submerged plants | rooted, erect emergent plants |
|--------------------------|---------------------------------|-----------------------------------|----------------------------------|
| 7.9. 83 Pond A | - | 4 (6) | 0 (6) |
| 7.12. 83 Pond C | - | - | 64 (10) |
| 1.2. 84 Pond C | 0 (8) | 83 (9) | 51 (7) |
| 23.2. 84 Pond A | 0 (7) | 0 (8) | 0 (17) |
| 29.2. 84 Uebeschiisee | 52 (20) | 53 (20) | 15 (20) |
| 10.4. 84 Pond C | 0 (10) | 165 (15) | 127 (15) |
| Total | 52 (45) | 305 (58) | 257 (75) |

MISCELLANEOUS OBSERVATIONS

Like other gerromorphan bugs, *M. furcata* can be fed in the laboratory with small insects both fresh and deep-frozen. In the field, specimens of *M. furcata* were observed several times feeding on plant lice and emerging midges. Mutual predation among gerromorphans was never actually seen in the wild but from obviously sucked out specimens in our samples, it can be inferred to happen. In the laboratory *M. furcata* is highly cannibalistic, hatching, moulting or newly moulted individuals being especially vulnerable.

At the end of June, a female with a parasitic water mite attached to the mesothorax was caught (not on one of our three ponds but on a small lake near Thun [Uebeschisee]). Some nymphs and adults of *G. paludum* and *G. argentatus* were in part heavily infested by larvae of the same mite species, which was probably *Limnochaes aquatica* (LUNDBLAD 1927, SPARING 1959, BOETTGER 1972).

A plant sample of September 7th contained eggs in which quite obviously a parasite had developed and "hatched". The pseudopericulum was still in place, but at the rear end of the eggs a circular hole existed. On February 29th, about 15 parasitized eggs were found in a plant sample from Uebeschisee. From March 28th onwards, adults of the hymenopte-

TABLE 5.
New localities in Switzerland, where we found *M. furcata*
(the 20th locality, pond C of our study, is omitted).

| Locality | Date | L1 | L2 | L3 | L4 | Adults | Total |
|------------------|-------|----|----|----|----|--------|-------|
| 1. Lobsigensee | 24.6. | 1 | 0 | 0 | 0 | 0 | 1 |
| " | 3.10. | 0 | 0 | 0 | 0 | 48 | 48 |
| 2. Uebeschisee | 30.6. | 9 | 16 | 6 | 27 | 30 | 88 |
| " | 20.7. | 11 | 16 | 15 | 14 | 21 | 77 |
| " | 12.9. | 2 | 1 | 6 | 21 | 68 | 98 |
| 3. Uttigen | 20.7. | 0 | 0 | 0 | 0 | 4 | 4 |
| 4. Rubigen | 8.8. | 3 | 3 | 2 | 3 | 4 | 15 |
| 5. Grandsivaz | 12.8. | 0 | 0 | 0 | 0 | 4 | 4 |
| 6. Payerne | 19.8. | 1 | 10 | 3 | 4 | 11 | 29 |
| 7. Cottens | 19.8. | 22 | 15 | 10 | 2 | 1 | 50 |
| 8. Entenmoos | 19.8. | 1 | 1 | 1 | 1 | 4 | 8 |
| 9. Kl. Moossee | 8.9. | 0 | 0 | 0 | 1 | 1 | 2 |
| 10. Häftli | 8.9. | 0 | 1 | 0 | 10 | 78 | 89 |
| 11. Alte Zihl | 8.9. | 0 | 0 | 1 | 37 | 62 | 100 |
| 12. Ansold.see | 12.9. | 1 | 1 | 1 | 3 | 23 | 29 |
| 13. Dittligsee | 12.9. | 0 | 0 | 0 | 4 | 16 | 20 |
| 14. Geistsee | 12.9. | 0 | 0 | 0 | 14 | 67 | 81 |
| 15. Gerzensee | 12.9. | 5 | 16 | 16 | 9 | 27 | 73 |
| 16. Chabrey | 13.9. | 1 | 2 | 1 | 3 | 64 | 71 |
| 17. Inkwilersee | 15.9. | 0 | 0 | 0 | 1 | 39 | 40 |
| 18. Burgäschisee | 15.9. | 1 | 1 | 0 | 0 | 16 | 18 |
| 19. Bellach | 15.9. | 0 | 0 | 0 | 1 | 52 | 53 |

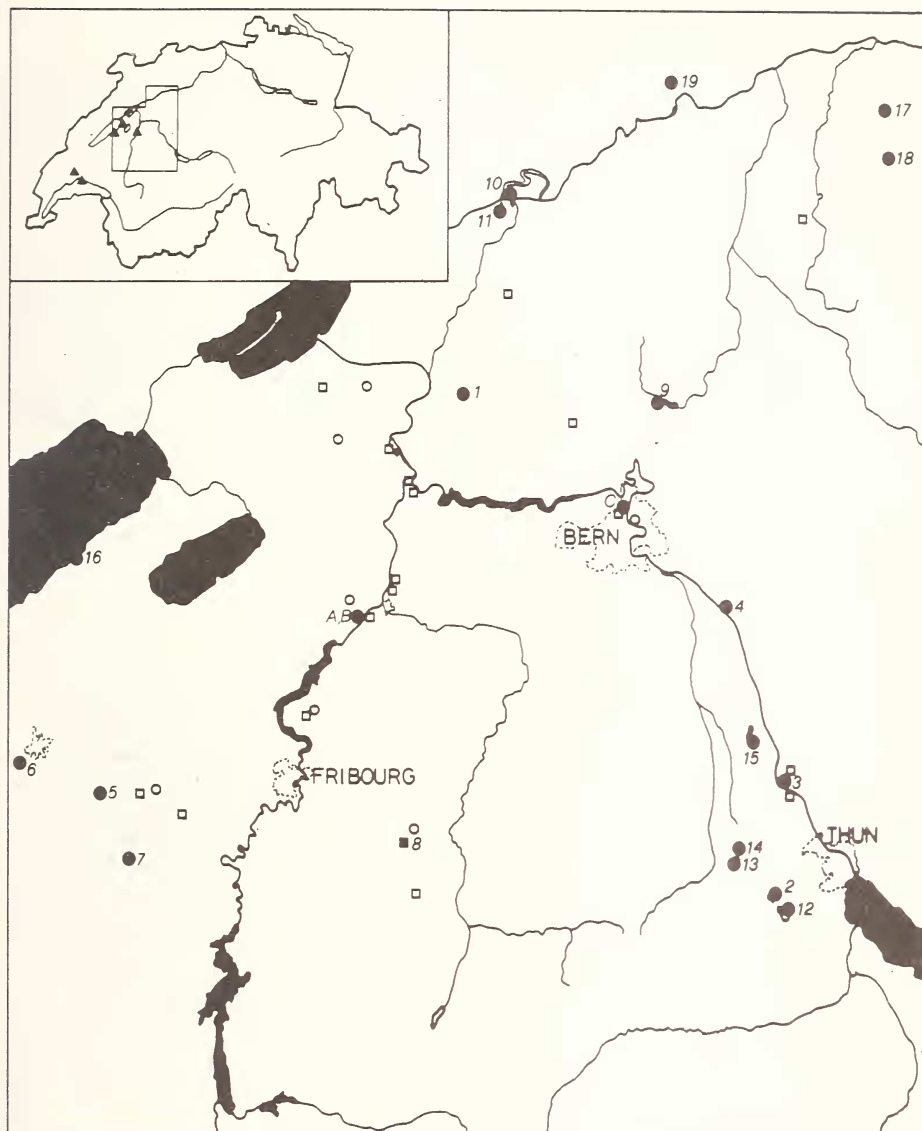


FIG. 4.

Distribution and habitats of *M. furcata* in the region Solothurn-Berne-Fribourg.

Open symbols: no *M. furcata* found

Closed symbols: *M. furcata* present

▲ (insert): published records of *M. furcata* in Switzerland (DETHIER & MATTHEY 1977, ZURWERRA 1978)

○ ● Localities where at least one species characteristic for the water lily communities (*Nymphaeion*) was found

□ ■ No characteristic members of *Nymphaeion* present. Numbers (1-19) correspond to the locality numbers in Table 5. A, B, and C: the three study ponds.

ran parasitoid *Anagrus incarnatus subfuscus* Hal. (Mymaridae) emerged from these eggs after gnawing a circular hole into the egg shell.

The adults and nymphs caught in the field were without wings or wing pads respectively. In laboratory cultures, however, winged specimens developed quite frequently. The same holds true according to our experience for the species *G. najas* and *Microvelia reticulata*, which too are generally wingless, at least in our region.

DISTRIBUTION AND HABITAT

The regional distribution of the pondweed bug in Switzerland is hardly known (Fig. 4). In addition to the five already known localities, 20 new ones were discovered, in 1983, in the region between Solothurn and Fribourg (Table 5), where *M. furcata* seems to be rather abundant. Most habitats of *M. furcata* in the explored region have a rich swimming vegetation composed mainly of *N. alba* and *Nuphar lutea* (Table 6). *M. furcata* was highly associated with plant species characteristic of the water lily communities (Nymphaeion) (OBERDORFER 1977) (Table 7). Generally *G. argentatus* ($C7=0,43\pm 0,12$, number of ponds=46) coexisted with the pondweed bug and *Microvelia reticulata* was negatively associated with *M. furcata* ($C7=-0,39\pm 0,17$; $C7$: coefficient of association, COLE 1949). On several occasions *Galerucella nymphaea*, *Donacia crassipes* and *D. versicolorea* (Chrysomelidae) were caught together with *M. furcata*.

TABLE 6.

Plants commonly found in the habitats of *M. furcata*.

- (1) DETHIER & MATTHEY 1977; (2) ZURWERRA 1978; (3) EKBLUM 1930; (4) JASTREY 1981; (5) NIESER 1981; (6) LUNDBLAD 1916, 1936; (7) BROWN 1948; (8) PEARCE & WALTON 1939; (9) WALTON 1943; (10) POISSON 1933; (11) SCHUMACHER 1919; (12) JANSSON 1916; (13) BOLLWEG 1915; (14) BUTLER 1893; (15) KUHLGATZ 1909; (16) STICHEL 1955; (17) WESENBERG-LUND 1943; (18) LINDBERG 1937; (19) TAMANINI 1979; (20) LINDBERG 1948; (21) BROWN 1943; (22) MAC GILLAVRY 1924; (23) GIBELLI & FERRERO 1891.

| plant species | number of own records | published records |
|---------------------------------|-----------------------|--|
| <i>Nymphaea alba</i> | 19 | 1, 3-6, 8, 10-12, 16-19, 22 |
| <i>Nuphar lutea</i> | 12 | 3, 6, 7, 11, 16, 18, 19 |
| <i>Potamogeton natans</i> | 5 | 2, 3, 6, 8, 9, 14 |
| <i>Polygonum amphibium</i> | 1 | 6, 8, 14, 19, 21, 22 |
| <i>Nymphoides peltata</i> | 0 | 1 |
| <i>Trapa natans</i> | 0 | 11, 23 |
| <i>Myriophyllum</i> sp. | 8 | 7, 18, 20 |
| <i>Potamogeton lucens</i> | 1 | 7, 8, 21, 22 |
| <i>P.</i> sp. | - | 1, 4, 5, 7, 10, 11, 13, 15, 16, 19, 20 |
| <i>Alisma plantago-aquatica</i> | 7 | 2, 8, 10, 14, 19, 20, 21 |
| <i>Lemna minor</i> | 4 | - |
| <i>Spirodela polyrrhiza</i> | 2 | 12 |
| <i>Elodea canadensis</i> | 3 | 8, 21 |
| <i>Hydrocharis morsus-ranae</i> | 0 | 11, 12, 16, 18 |

TABLE 7.

Association of *M. furcata* with water lily communities (Nymphaeion).

N+ at least one species characteristic of **Nymphaeion** present

N- no member of the **Nymphaeion** found

M+ *M. furcata* present

M- no pondweed bugs found

C7 COLE's (1949) coefficient of association

$\chi^2=24,31$; $C7=0,89\pm 0,16$

| | N+ | N- | S |
|----|----|----|----|
| M+ | 25 | 1 | 26 |
| M- | 7 | 17 | 24 |
| S | 32 | 18 | 50 |

DISCUSSION

First instar nymphs from our field samples and laboratory rearings correspond in their morphology and chaetotaxy to the descriptions and figures given by LUNDBLAD (1916a), TEYROVSKY (1920) and COBBEN (1978). The first instar of *M. furcata* is very similar to that of *M. vittigera* (ANDERSEN 1982) and also of the three nearctic and neotropical species *M. mulsanti*, *M. amoena* and *M. cryptophila* (HUNGERFORD 1917, 1919, HOFFMANN 1932). Biometry and morphology of our fourth instar are in accordance with the data given in the literature for last instar nymphs (BOLLWEG 1915, SCHOUTEDEN 1921, JORDAN 1931, 1936, EKBLOM 1930, STUSAK 1980, ANDERSEN 1982).

At present no published records are known where five different nymphal stages were ever caught together in one and the same sample (e.g. DETHIER & MATTHEY 1977, NIESER 1981). As a rule, the number of nymphal stages is fixed in gerromorphan bugs. So far, only *Microvelia pulchella* is known to have either four or five preimaginal instars, the factors determining the actual number being unknown (FRICK 1949, ANDERSEN 1982). If it cannot be ascertained that *M. furcata* is another such exception, it is from our findings obvious that this species develops through only four nymphal instars.

Published records of nymphs and adults of *M. furcata* sampled in the field are summarized in Table 8. Young nymphs are reported from Central Europe from May to August and adults between May and October (HORVATH 1915). We might, therefore, conclude that *M. furcata* has generally more than one generation per year, most probably three as found in our study. A serious analysis of voltinism requires periodical observations. As no such studies have been published so far, generation number is commonly underestimated (e.g. DETHIER & MATTHEY 1977). The few young nymphs caught in September and October even suggest a partial fourth generation. Under laboratory conditions a small fraction of eggs laid by third generation females developed directly without prior diapause (Table 3).

TABLE 8.

Seasonal occurrence of nymphs and adults of *M. furcata* in Central Europe according to different authors.

- (1) NIESER 1981; (2) ZURWERRA 1978; (3) DETHIER & MATTHEY 1977; (4) DETHIER 1975;
 (5) MAC GILLAVRY 1924; (6) BRINKHURST 1959; (7) BROWN 1948; (8) WALTON 1943;
 (9) PEARCE & WALTON 1939; (10) MUELLER 1919; (11) JORDAN 1936; (12) EKBLUM 1930;
 (13) LUNDBLAD 1915; (14) LUNDBLAD 1916; (15) BOLLWEG 1915; (16) LINDBERG 1948;
 (17) GULDE 1921; (18) POISSON 1933; (19) BUTLER 1923; (20) JANSSON 1916;
 (21) JACZEWSKI 1922; (22) KUHLGATZ 1911; (23) LUNDBLAD 1916a; (24) HORVATH 1915.

| month | young nymphs (L1, L2) | old nymphs (L3, L4) | nymphs | adults |
|-----------|--------------------------|------------------------|-----------------------|----------------------------------|
| May | | | 18, 24 | 24 |
| | 8, 15 | | 18, 24 | 24 |
| June | | 11 | 13, 18 | 11, 21, 24 |
| | 22, 23 | | 13, 14, 18 | 13, 15, 24 |
| July | 5 | 1 | 3, 10, 14, 18, 21, 24 | 1, 3, 14, 18, 21, 24 |
| | 15 | 12 | 3, 14, 16, 18, 21, 24 | 3, 5, 15, 18, 21, 24 |
| August | 1, 22 | 1, 22 | 7, 19 | 1, 3, 9, 13, 14, 17, 18, 22, 24 |
| | | 1 | 3, 19 | 1, 2, 3, 6, 9, 17, 18, 24 |
| September | | | 7 | 4, 9, 14, 17, 18, 19, 20, 21, 24 |
| | | | | 2, 4, 7, 9, 14, 18, 20, 24 |

Observed stage durations in laboratory cultures (27° C, 18L:6D) (L1: 3d; L2: 4d; L3: 3,5d; L4: 7d) correspond quite well with those estimated for free living second generation instars. Overall survival in three mass cultures ranged between 0,38 and 0,46. Mortality of all nymphal instars was about the same. The general assumptions of the method of KIRITANI and NAKASUJI extended by MANLY (1976) and its applicability are discussed by SOUTHWOOD (1978) and ZIMMERMANN *et al.* (1982).

In our laboratory cultures, females of the second generation already laid about 50% diapause eggs. As in other species with an embryonic diapause (BECK 1980), diapause in *M. furcata* is probably also determined by experiences of photoperiods and temperatures by the parental generation. GALBREATH (1976) showed that in *M. mulsanti* diapause, which occurs in the same developmental stage as in *M. furcata* (GALBREATH 1973), among

other influences, depends on the age of the ovipositing female. Whether 2nd generation females lay diapause eggs in the field remains open to question.

The controversy: hibernating as eggs versus hibernating as adults, pertains not only to *M. furcata* but to *M. mulsanti* as well. The early observations by HOFFMANN (1932) suggested overwintering in the egg stage, and GALBREATH (1973, 1975, 1976) unequivocally proved this to be so. But even in the more recent literature (BROOKS & KELTON 1967, PENNAK 1978), the imago is reported to hibernate. Our observations are in full agreement with those of GALBREATH, and therefore it seems safe to say that *M. furcata* hibernate in an embryonic diapause. Eggs can hibernate under quite different conditions: in rotting plants at the bottom of ponds, in rooted upright submerged plants at times surrounded by ice and in emergent vegetation above the water surface exposed to considerable variations of temperature. This is in contradiction to EKBLÖM (1930) who found eggs only in rotting plants, and states that *M. furcata* never inserts eggs into plants in upright position.

The egg parasitoid *Anagrus incarnatus subfuscus* Hal. (DEBAUCHE 1948) is reported to attack the eggs of several species of damselflies, Odonata (*Coenagrion pulchellum*, *Calopteryx virgo*, *Lestes* sp.) (HENRIKSEN 1922, BAKKENDORF 1925, BERTRAND 1954). Obviously depending on host egg size *A. incarnatus* is either solitary (ARDITI 1980), only one parasitoid larva developing in the host egg, like in *M. furcata*, or gregarious, several larvae developing simultaneously within the same egg (BAKKENDORF 1925). *A. i. subfuscus* hibernates within the host eggs (BAKKENDORF 1925, HEDQVIST 1978, and our own observations). Another hymenopteran parasitoid, *Hydrophylax aquivolans* (Trichogrammatidae), is known to develop both in eggs of *Ischnura* sp. (Odonata) and those of *M. mulsanti* (HOFFMANN 1932a).

SCHUMACHER (1919) already suggested that *M. furcata* might not be as rare as commonly assumed, if only they were looked for at the right places: small lakes with abundant swimming vegetation. Our results fully confirm this prognosis. *M. furcata* was found to be abundant on brackish water, too (LINDBERG 1948). PEUS (1932) suggests that the pondweed bug is tyrphoxene. Neither did we find *M. furcata* on peat bogs in the Swiss Jura mountains, even when a rich swimming vegetation would have favoured their presence. Virtually nothing is known about wing length determination and adaptive value of wing polymorphism in *M. furcata*. The conclusions of ZERA, INNES and SAKS (1983): "Until more detailed information for both the genetic and environmental components of wing polymorphism become available, it will not be possible to formulate realistic models of the evolution of winglessness." are not only valid for gerrids but for mesoveliids and veliids as well (cf. GALBREATH 1975).

ZUSAMMENFASSUNG

Auf drei Weihern in der Umgebung von Bern untersuchten wir die Populationsstruktur und den Lebenszyklus des Hüftwasserläufers *Mesovelia furcata* (Hemiptera, Mesoveliidae). Zuchten unter kontrollierten Bedingungen im Labor unterstützten unsere Feldbeobachtungen.

In unseren Feldstichproben (ca 3000 Larven), in Massenkulturen der verschiedenen Stadien, vor allem aber bei einzeln aufgezogenen Larven fanden wir nur vier Larvenstadien, eine ungewöhnliche Anzahl für semiaquatische Wanzen (Gerromorpha).

M. furcata war klar trivoltin. Der Hüftwasserläufer überwintert als Ei in einer embryonalen Diapause. Diapause-Eier unterbrechen ihre weitere Entwicklung, wenn der Keimstreifen (in den Dotter eingesenkt) eine S-Form erreicht hat. Symbionten bilden einen roten Ring unter dem Pseudopericulum. Weibchen der ersten Generation legten im Labor (24° C,

18L:6D) nur Subitan-Eier. Bereits Weibchen der zweiten Generation legten Diapause-Eier (ca 50%). Weibchen der dritten Generation legten praktisch nur noch Diapause-Eier, die sich unter den angegebenen Bedingungen nicht mehr weiter entwickelten. Eine sechswöchige Kältebehandlung beendete die Diapauseentwicklung. *M. furcata* überwintert im Ei-stadium sowohl in wurzelnden Pflanzen über und unter dem Wasserspiegel, als auch in verfaulenden Pflanzenfragmenten am Grunde der Weiher. *Anagrus incarnatus subfuscus* Hal. (Hymenoptera, Mymaridae), ein Eiparasitoid in Odonaten, befällt nach unseren eigenen Beobachtungen auch die Eier von *M. furcata*, wo er auch überwintern kann.

M. furcata ist im Untersuchungsgebiet weit verbreitet und stark an Seerosendecken (Nymphaeion) gebunden.

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